

MORPHOLOGICAL VARIATION AMONG MIGRATORY AND NON-MIGRATORY POPULATIONS OF PRAIRIE WARBLERS

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ABSTRACT.—The two subspecies of Prairie Warblers (*Dendroica discolor*) differ in migratory behavior and habitat use. A concurrent study of mitochondrial DNA variation showed that behavioral differences between subspecies may persist because little gene flow occurs between subspecies. To determine whether geographic variation in morphology parallels variation in migratory behavior and mitochondrial DNA, I used measurements of museum specimens from throughout the Prairie Warbler's range. The subspecies differ in overall body size, with birds of the Florida subspecies (*D. d. paludicola*) significantly larger than the nominate race. Males of the subspecies differ in the extent of white coloration in the outer rectrices. These differences were apparent even among specimens collected in northern Florida and southern Georgia, where the subspecies' ranges are most proximate. Morphological differences coincide with differences in behavior and mitochondrial DNA and support the recognition of migratory and non-migratory forms of Prairie Warblers as subspecies and as potentially independent evolutionary lineages. Received 21 May 1999, accepted 23 Oct. 1999.

Prairie Warblers (*Dendroica discolor*) consist of two geographically separated subspecies that differ in migratory behavior and habitat use (Nolan 1978). One subspecies (*D. d. discolor*) is migratory between its breeding range in the eastern United States (south to northern Florida) and its winter range in Florida and the West Indies (Nolan 1978). *Dendroica d. discolor* is a habitat generalist and is found in southern pine (*Pinus*) forests, forest-grassland edges, abandoned fields, dunes, and other early successional habitats (Nolan 1978). The other subspecies (*D. d. paludicola*) is non-migratory and is restricted throughout the year to mangroves in subtropical Florida (Robertson and Woolfenden 1992, Stevenson and Anderson 1994).

Because the geographic distribution of heritable phenotypic variation is in part determined by underlying patterns of gene flow, discontinuous variation is usually restricted to interspecific differences, whereas intraspecific geographic variation is more commonly continuous and expressed as a cline (Zink and Remsen 1986). Given previous demonstrations of significant genetic contributions to inter-population differences in migratory behavior (Berthold and Helbig 1992), the geographic distribution of migratory and non-migratory Prairie Warblers suggests that there is little

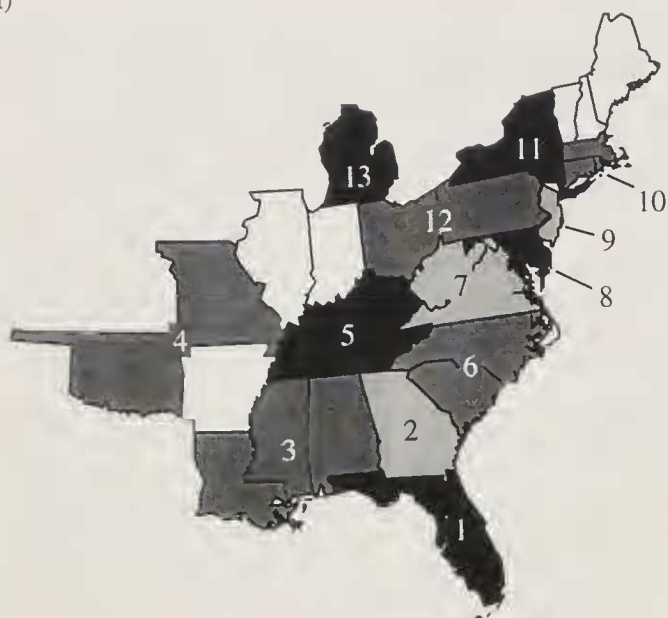
gene flow between *D. d. discolor* and *D. d. paludicola*. Limited gene flow across the relatively small distance (ca 200 km) separating the breeding ranges of two subspecies would be surprising given the capacity for long distance movements by Prairie Warblers and the observation that some *D. d. discolor* migrate to Florida for the non-breeding season (Stevenson and Anderson 1994). On the other hand, genetic isolation might be expected based on the disparate breeding habitats used by the two subspecies.

In a concurrent study of the distribution of mitochondrial (mt) DNA variation, I found evidence for reduced gene flow, but no well supported phylogenetic distinction between the subspecies (Buerkle 1999). Ideally, multiple independent genetic loci would be used to address this question. However, in the absence of additional genetic data, morphology can provide "surrogate genetic information" to studies of intraspecific phylogeny and geographic variation (Avice 1994:242). The use of morphological characters requires consideration of environmental influences on development, but morphological variation may reflect underlying genetic variation (e.g., Boag 1983). Substantial differences in morphology between migratory and non-migratory Prairie Warblers would be consistent with an interruption of gene flow between *D. d. discolor* and *D. d. paludicola*. Because they may have different evolutionary histories, it is not necessary that all three classes of characters (morphological, genetic, and behavioral) co-

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a)



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FIG. 1. Geographic regions used to pool (a) male and (b) female specimens. Shades of gray are used to differentiate adjacent regions. States without shading are not represented in this study. Number of male specimens from each region (in ascending numerical order): 19, 20, 8, 13, 16, 17, 12, 16, 23, 13, 10, 8, 27. Number of female specimens from each region (in ascending numerical order): 8, 8, 5, 9, 11, 8, 11.

vary geographically. However, concordance among them would support the hypothesis that despite their geographic proximity, migratory and non-migratory subspecies of Prairie Warblers are isolated from one another and may continue to diverge.

Previous descriptions of the morphology of Prairie Warbler subspecies have not identified any plumage or other morphological characters that can be reliably used to identify sub-

species (see Howell 1930, Nolan 1978). Howell's (1930) description of *D. d. paludicola* is generally consistent with the morphology of many individuals of *D. d. discolor*, and it is possible that he recognized the Florida Prairie Warbler as a separate subspecies based partially on its unusual breeding habitat. Howell (1930) referred to *D. d. paludicola* as a common breeder and did not mention the subspecies' migratory status.

In this paper I describe morphological variation among populations of Prairie Warblers, with the goal of determining whether the geographic distribution of morphological variation is coincident with the difference in migratory behavior and mtDNA variation. I used morphological data obtained from measurements of Prairie Warbler specimens in museum collections to determine the pattern of geographic variation. In particular, I used multivariate analyses to evaluate the distinctiveness of the Florida subspecies and to determine whether the pattern of morphological variation offers additional evidence for a reduction of gene flow between *D. d. paludicola* and *D. d. discolor*.

METHODS

From the collections of nine institutions (see Acknowledgments), I selected specimens collected between 1 May and 31 August, 1869–1989. Specimens available from Florida were collected between 6 May and 23 June. A small number of the birds at the extremes of the 1 May to 31 August period may have been migrants; however, based on dates of migration from Nolan (1978), this sample should contain primarily breeding residents. Error introduced by migrants would tend to obscure variation among locations.

In selecting specimens I gathered birds collected from locations across the range of the species, which I then grouped into general geographic regions. It would be preferable to have a number of specimens from single locations (i.e., point samples); however, this was not possible with existing specimens. Because of known sexual dimorphism (Nolan 1978, and confirmed with these specimens), I considered females and males separately. Collections contained far fewer female specimens than male, therefore I used separate schemes for defining geographic regions for males and females. While attempting to minimize the size of regions, I grouped specimens into regions so that each region contained approximately 10 or more specimens and roughly equal numbers of individuals. Specimens were first grouped by state in which they were collected; then adjacent states with fewer than 10 specimens were pooled (Fig. 1). This method of pooling

TABLE 1. Character correlation matrix for males (below diagonal) and females (above diagonal).

	Bwidth	Eculmen	Culmen	Rectrix4	Rectrix5	Rectrix6	Tail	Tarsus	Toe	Wing
Bwidth	—	0.476	0.313	0.224	0.060	0.203	0.258	0.387	0.391	0.217
Eculmen	0.340	—	0.730	−0.002	−0.034	−0.040	0.158	0.427	0.368	0.127
Culmen	0.400	0.646	—	−0.047	−0.079	−0.089	0.295	0.323	0.323	0.134
Rectrix4	0.064	0.074	0.045	—	0.644	0.430	0.285	0.208	0.078	0.402
Rectrix5	0.057	0.012	0.081	0.735	—	0.547	0.324	0.224	0.330	0.434
Rectrix6	0.084	0.089	0.114	0.518	0.708	—	0.383	0.183	0.244	0.109
Tail	0.143	0.201	0.324	0.172	0.189	0.220	—	0.392	0.559	0.585
Tarsus	0.153	0.243	0.168	−0.103	−0.076	0.077	0.252	—	0.531	0.318
Toe	0.174	0.265	0.263	−0.049	−0.049	0.037	0.307	0.469	—	0.484
Wing	0.058	−0.003	0.134	0.359	0.340	0.324	0.458	0.123	0.090	—

specimens is conservative and any error will tend to obscure variation among locations.

The sex of specimens was taken from muscum tags and confirmed using criteria based on plumage coloration in Nolan (1978). These were rarely in disagreement. Based on plumage coloration, a few specimens were obviously not the sex they had been labeled, and in these cases I relied on plumage criteria in Nolan (1978) for determining sex. I distinguished between hatching-year birds (in first basic plumage and prior to 31 December) and after-hatching-year birds (birds in at least their second calendar year) based on plumage characteristics (Nolan 1978). Very few hatching-year birds were available and the analysis below is of after-hatching-year birds only.

I measured 11 characters on study skins: (1) Wing, wing chord length of unflattened wing from anterior bend in the wing to tip of longest primary; (2) Tail, length of central rectrices from insertion point to tip; (3) Bdepth, depth of bill measured from upper to lower mandible at anterior edge of the nares; (4) Bwidth, width of bill measured at anterior edge of the nares; (5) Eculmen, chord length of exposed culmen measured along bill axis from the edge of feathering at base of bill to tip of upper mandible; (6) Culmen,

chord length of bill from anterior edge of nares to tip of the upper mandible; (7) Rectrix4, length of white area along rachis of fourth rectrix (rectrix otherwise blackish); (8) Rectrix5, length of white on fifth rectrix; (9) Rectrix6, length of white on sixth (outermost) rectrix; (10) Tarsus, tarsus length measured diagonally from the posterior surface of the metatarsus to the anterior margin of the last scute on the metatarsus; (11) Toe, length of hind toe including claw, from base on dorsal surface of the digit to tip of claw (terminology follows Zink 1986, Pyle et al. 1987, Atwood 1988). All of these, except for tail length, were measured with digital calipers and recorded to the nearest 0.01 mm. I measured tail length with a ruler inserted between central rectrices and recorded values to the nearest 0.5 mm. (Univariate descriptive statistics and numbers of individuals measured for each character are available from the author upon request.)

I did not measure all characters for specimens with features that were either missing or damaged, and I did not measure heavily damaged specimens. Otherwise, all specimens were measured and included in the analysis. Out of 269 specimens, 1 had six missing characters, 4 had four missing characters, and 2 had three missing characters; all others had two or fewer missing

TABLE 2. Loading of variables on first five principal components for males. Eigenvalues, percentage of variation accounted for by each principal component, and the cumulative percentage of variation explained.

	PC1	PC2	PC3	PC4	PC5
Bwidth	0.388	0.390	−0.411	−0.017	0.721
Eculmen	0.465	0.560	−0.437	0.038	−0.342
Culmen	0.544	0.530	−0.396	−0.213	−0.219
Rectrix4	0.626	−0.560	−0.140	0.105	−0.027
Rectrix5	0.674	−0.600	−0.117	0.200	−0.023
Rectrix6	0.680	−0.432	−0.027	0.299	−0.026
Tail	0.610	0.191	0.391	−0.442	−0.070
Tarsus	0.311	0.510	0.479	0.415	0.088
Toe	0.356	0.544	0.399	0.334	−0.034
Wing	0.586	−0.205	0.397	−0.474	0.130
Eigenvalue	2.910	2.241	1.251	0.891	0.717
% of Variance	29.1	22.4	12.5	8.9	7.2
Cum. % of Var.	29.1	51.5	64.0	72.9	80.1

TABLE 3. Loading of variables on first five principal components for females. Eigenvalues, percentage of variation accounted for by each principal component, and the cumulative percentage of variation explained.

	PC1	PC2	PC3	PC4	PC5
Bwidth	0.577	0.303	0.400	−0.096	−0.514
Eculmen	0.507	0.692	0.280	0.182	0.151
Culmen	0.458	0.683	0.076	0.225	0.425
Rectrix4	0.513	−0.564	0.330	0.446	−0.080
Rectrix5	0.568	−0.633	0.118	0.149	0.177
Rectrix6	0.474	−0.521	0.391	−0.446	0.265
Tail	0.740	−0.105	−0.378	−0.161	0.179
Tarsus	0.685	0.222	0.017	−0.163	−0.203
Toe	0.757	0.153	−0.297	−0.320	−0.043
Wing	0.669	−0.199	−0.501	0.346	−0.181
Eigenvalue	3.647	2.150	1.002	0.788	0.683
% of Variance	36.5	21.5	10.0	7.9	6.8
Cum. % of Var.	36.5	58.0	68.0	75.9	82.7

characters. Bill depth was not used in the multivariate analyses because it was missing from 21.3% of females and 24.5% of males. Observations for other characters were missing from less than 5% of individuals.

I used principal components analysis (PCA) to extract a limited number of independent variables from the measured characters (FACTOR procedure; SPSS version 6.1 for Macintosh; SPSS Inc. 1995). In calculating principal components, I substituted the grand mean for missing characters. This procedure is conservative in that it will tend to reduce variation among populations; yet it allowed me to include information from a greater number of specimens. Using principal component scores as the dependent variable, I performed an analysis of variance (ANOVA) to test for variation among regions (ONEWAY procedure; SPSS Inc. 1995). I also performed two planned comparisons to test for the distinctiveness of Florida Prairie Warblers: Florida mean versus the average of the means of all other regions, and Florida mean versus Georgia mean (CONTRAST procedure; SPSS 1995).

RESULTS

Several of the measured characters were highly correlated, while others were not (Table 1). Principal Components Analysis resulted in three factors with eigenvalues greater than one (Tables 2, 3), and only these are considered here because the remaining factors explained less of the variation among individuals than did the individual original variables (Norusis 1994). The first three PC factors together explained 64% and 68% of the total variance for males and females, respectively.

All measured variables were positively correlated with PC1 for both males and females, suggesting that PC1 corresponds to overall body size (Tables 2, 3). The contribution of various characters to PC2 differed between males and females (Tables 2, 3). For males, large positive values for PC2 corresponded to small amounts of white in the rectrices (Rec-

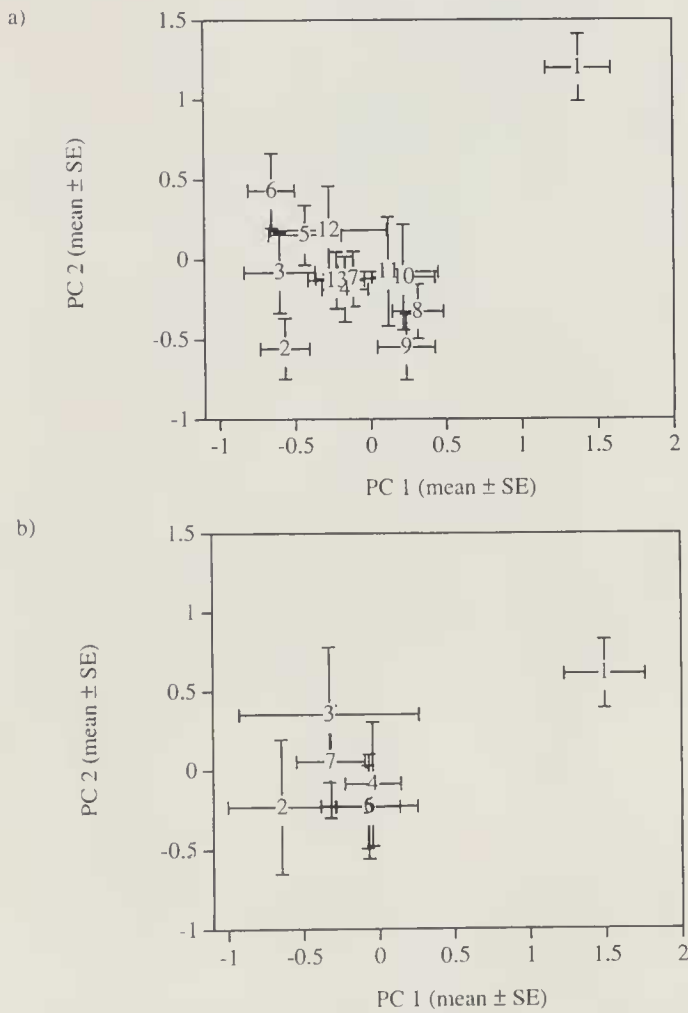


FIG. 2. Plots for (a) males and (b) females of PC1 versus PC2 for region means ($\pm$ SE). Numbers used to identify regions are the same as in Fig. 1. Labels for regions 5 and 6 overlap in the plot for females.

TABLE 4. ANOVA and planned comparison results for principal component scores for males. Regions refer to geographic regions described in Fig. 1. Planned comparisons utilize separate variance estimates and an approximate *t*-test (Lindman 1992). ω^2 refers to the proportion of total variation that is accounted for by differences between regions.

Source	df	MS	F	P	ω^2_{bet}
PC1					
Between Regions	12	5.150	7.120	<0.001	0.267
Within Regions	189	0.723			
Total	201				
	<i>t</i>	df	P		
Florida vs Other	6.930	21.7	<0.001		
Florida vs Georgia	7.213	34.1	<0.001		
	df	MS	F	P	ω^2_{bet}
PC2					
Between Regions	12	3.927	4.987	<0.001	0.192
Within Regions	189	0.788			
Total	201				
	<i>t</i>	df	P		
Florida vs Other	5.954	22.0	<0.001		
Florida vs Georgia	6.187	36.5	<0.001		
	df	MS	F	P	ω^2_{bet}
PC3					
Between Regions	12	3.623	4.324	<0.001	0.165
Within Regions	189	0.838			
Total	201				
	<i>t</i>	df	P		
Florida vs Other	1.06	23.7	0.300		
Florida vs Georgia	2.67	36.8	0.011		

trix4–Rectrix6) and large dimensions for all other variables except for wing length (Table 2). Negative values for PC2 corresponded to larger amounts of white in the tail and smaller overall body proportions (except for Wing). Similarly, for females the amount of white in the rectrices (Rectrix4–Rectrix6) was highly negatively correlated with PC2, bill dimensions were highly correlated positively, and other dimensions had smaller correlations with PC2 (Table 3). For males, bill dimensions were negatively correlated with PC3 and four other variables (Tail, Tarsus, Toe, Wing) were positively correlated (Table 2). For females, wing, toe, and tail lengths were negatively correlated with PC3 and other dimensions had either low or positive correlations (Table 3).

Bivariate plots of regional means for principal component scores suggested that birds from Florida (Region 1) were distinct from those from the remaining regions (Fig. 2). The

disjunction was evident on both PC1 and PC2 for males, whereas females from Florida appeared to differ from the remaining regions only on PC1. The obvious graphical differences on PC1 and PC2 for males, and on PC1 for females, were statistically significant in the analysis of variance and planned comparisons (males: Table 4; females: Table 5). According to the differences on PC1, *D. d. paludicola* males and females generally are larger than *D. d. discolor* individuals. On the second PC axis Florida males had the largest positive scores ($\bar{x}$ = 1.19, Fig. 2a), indicating that Florida males had less white in their tails relative to their overall body size. In comparison, *D. d. discolor* males had smaller scores (range of means: −0.56–0.42), that are indicative of a smaller disparity in the amount of white relative to body size. For females, less of the variation in PC2 was associated with differences among regions and only the comparison

TABLE 5. ANOVA and planned comparison results for principal component scores for females. Regions refer to geographic regions described in Fig. 1. Planned comparisons utilize separate variance estimates and an approximate *t*-test (Lindman 1992). ω^2 refers to the proportion of total variation that is accounted for by differences between regions.

Source	df	MS	F	P	ω^2_{bet}
PC1					
Between Regions	6	3.831	5.485	<0.001	0.310
Within Regions	53	0.698			
Total	59				
	<i>t</i>	df	<i>P</i>		
Florida vs Other	−5.777	11.1	<0.001		
Florida vs Georgia	−4.822	13.0	<0.001		
Source	df	MS	F	P	ω^2_{bet}
PC2					
Between Regions	6	0.848	0.819	0.560	0
Within Regions	53	1.035			
Total	59				
	<i>t</i>	df	<i>P</i>		
Florida vs Other	−2.518	14.6	0.024		
Florida vs Georgia	−1.763	10.5	0.107		
Source	df	MS	F	P	ω^2_{bet}
PC3					
Between Regions	6	1.511	1.738	0.130	0.069
Within Regions	53	0.870			
Total	59				
	<i>t</i>	df	<i>P</i>		
Florida vs Other	0.232	8.5	0.822		
Florida vs Georgia	0.774	12.4	0.453		

of PC2 means between Florida and all other regions pooled was significant (Table 5). Similar plots of regional means for PC2 and PC3 indicated that for PC3 the Florida means for males and females fell within the range of means from the other regions (Fig. 3). Means for male specimens on PC3 did not differ between Florida and all other regions pooled, but the Florida mean was different from the Georgia mean (Table 4). For females, none of the comparisons involving PC3 was significant (Table 5).

DISCUSSION

Morphological differences between *D. d. paludicola* and *D. d. discolor* parallel differences in behavior (migratory tendency and habitat use) and mtDNA (Buerkle 1999). With respect to avian taxonomy, the observed morphological differences are consistent in magnitude with those between typical avian subspecies (Morrison 1983, Ball and Avise

1992). However, the concordance among independent classes of characters suggests that *D. d. paludicola* and *D. d. discolor* may represent relatively distinct evolutionary lineages that harbor disparate evolutionary potentials and may continue to diverge over time. This study and others (e.g., Avise and Nelson 1989, Rising and Avise 1993) demonstrate that significant boundaries among populations of birds are not necessarily associated with obvious geographic barriers to dispersal, and that morphological differences may be cryptic and need not include plumage differences that are easily observed by humans. The two primary differences found in the PCA can be summarized as follows: Florida Prairie Warblers are larger than *D. d. discolor* individuals, and males of *D. d. paludicola* have less white in the tail. The functional aspects of the size difference may be related to both migratory behavior and habitat use because these behaviors may constrain one an-

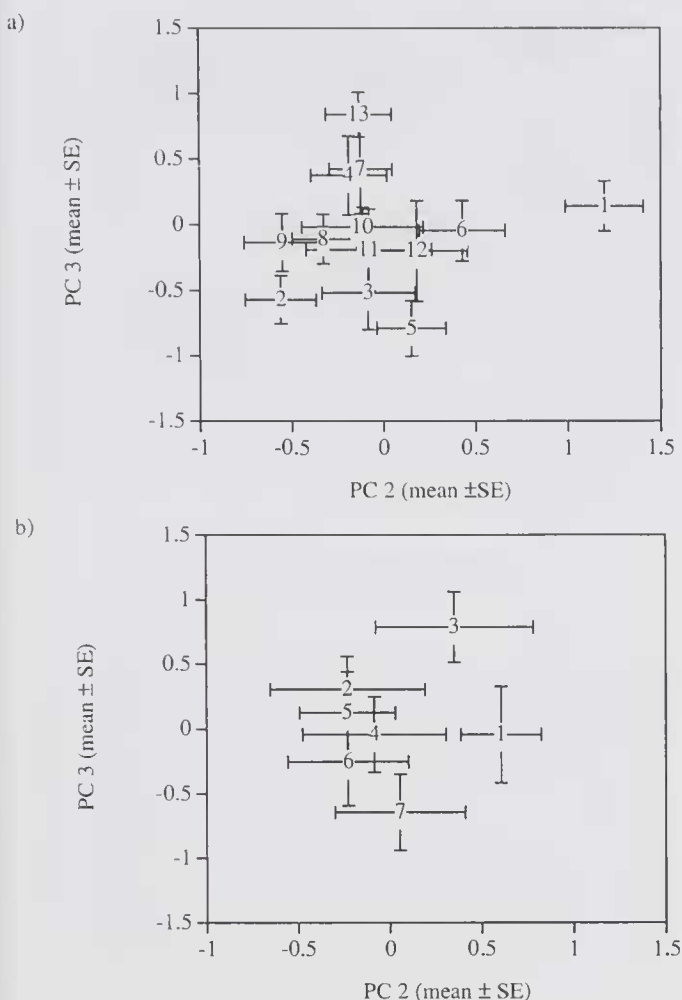


FIG. 3. Plots for (a) males and (b) females of PC2 versus PC3 for region means ($\pm$ SE). Numbers used to identify regions are the same as in Fig. 1.

other through morphology (Winkler and Leisler 1992). Migration distance is positively correlated with wing length in parulids (Parulidae including *Dendroica*; Winkler and Leisler 1992), as is openness of habitat (or vegetation height) in Old World warblers (Sylviidae) and other avian families (Zink and Remsen 1986, Winkler and Leisler 1992). Although a trend for increasing wing length with latitude and migration distance was evident (unpubl. data), this does not explain the overall larger size of *D. d. paludicola*. It is possible that differences between subspecies are related to differences in migratory behavior and habitat use, but an understanding of that relationship requires further study.

The difference between male *D. d. paludicola* and *D. d. discolor* in the amount of white in the tail may be related to the potential role of the tail, and particularly the conspicuous white area, in intra- and intersexual behavior (Nolan 1978). Prairie Warblers commonly fan

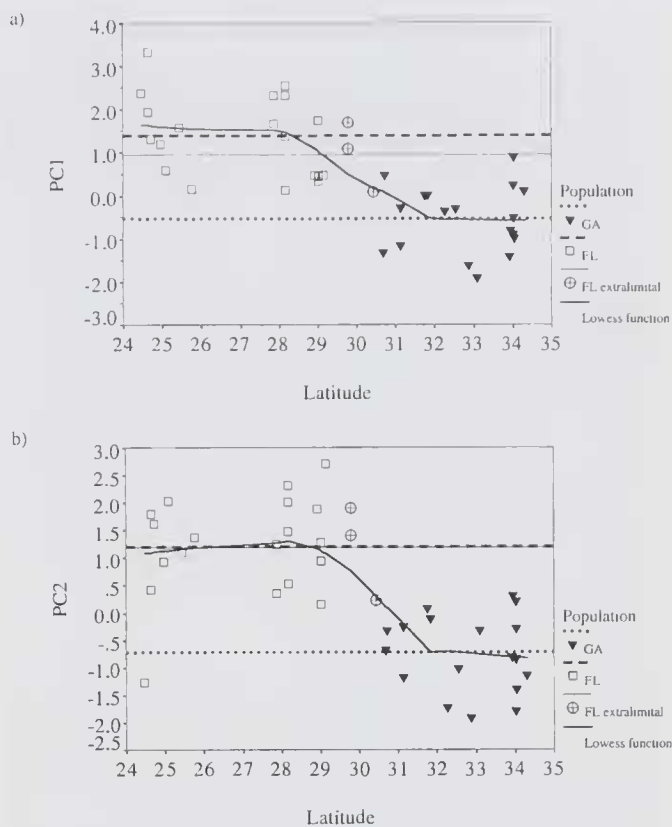


FIG. 4. Plots of (a) PC1 and (b) PC2 versus latitude for male specimens from Florida and Georgia. Horizontal lines indicate group means. Lowess line is based on a locally weighted least squares regression (local fit of line to 50% of data points; SPSS Inc. 1995). Latitude data were obtained by using locality information on museum tags and the Geographic Names Information System of the United States Geological Survey. Specimens with ambiguous locality information were excluded. Three Florida specimens from outside the known range of *D. d. paludicola* are coded as FL extralimital.

their tails in display flights during territorial encounters and courtship (Nolan 1978); differences in the function or performance of either type of behavior could result in morphological divergence. In interpreting the functional significance of morphological differences described here, it must be kept in mind that the analysis is a fairly limited description of Prairie Warbler morphology. The limited number of variables I measured served the purpose of differentiation between taxa. However, their utility for understanding the possible role of selection in shaping differences is limited. Detailed study of behavioral and habitat differences might indicate which morphological variables should be compared to better understand the potential role of adaptation.

One striking feature of the comparisons of regional means is the difference between the

Florida and Georgia populations (Fig. 2). In addition to the differences in means between birds from Georgia and Florida, there is generally little overlap of the principal component scores of individual male specimens from these regions (Fig. 4). The differences in means between regions are evident even among individuals separated by approximately 200 km. Included in Fig. 4 are three specimens from locations in Florida that lack mangroves typical of peninsular Florida (Tallahassee, coastal Dog Island south of Tallahassee). The two specimens from Dog Island (upper two on PC1 and PC2; Tall Timbers Research Station specimens #2895 and #2897) were collected in mid-June eleven years apart and may represent *D. d. paludicola* vagrants along the Gulf Coast. Dog Island supports an isolated, stunted black mangrove (*Avicennia germinans*) community, not the typical mangrove communities along the peninsular Gulf Coast, which are more diverse and consist of taller trees (Sherrod and McMillan 1983). Because the Dog Island specimens were missing data for the white in the tail (Rectrix4–Rectrix6), their affinity to either group was not tested with discriminant function analysis. The specimen from Tallahassee (Smithsonian Institution #599804) was probably a migrant. It was killed by a nocturnal collision with a television tower (1 May) and had a large amount of subcutaneous fat.

Because of its rarity and restricted range, the status of *D. d. paludicola* populations is of concern (Florida Natural Areas Inventory 1995). Evidence for the morphological distinctiveness of *D. d. paludicola*, along with divergent behavior and genetics, suggests that the two Prairie Warbler subspecies are likely to have distinct evolutionary potentials. Recognition of such evolutionarily significant units can aid in defining conservation priorities (Moritz 1994, Lesica and Allendorf 1995). Suitable habitat for *D. d. paludicola* is very limited because populations are restricted to mangroves and do not breed inland (Robertson and Woolfenden 1992, Stevenson and Anderson 1994). In addition, land development has substantially reduced or modified mangrove habitat with 90% of the remaining acreage in the four southernmost counties in the state (Gilmore and Snedaker 1993). Given that Florida Prairie Warblers are one of very

few land birds that breed in mangroves (Robertson 1955, Robertson and Kushlan 1974), their status should be considered when evaluating acquisitions of mangrove habitat for protection.

The substantial discontinuity between birds of Florida and of the remaining regions is the most conspicuous feature of geographic variation in Prairie Warbler morphology. The results support previous taxonomic recognition of *D. d. paludicola* and *D. d. discolor* as subspecies and suggest the potential for further evolutionary divergence.

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